

EFFECTS OF CONTEXTUAL INFORMATION ON BEHAVIOR OF *CALIDRIS* SANDPIPERS FOLLOWING ALARM CALLS

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Two classes of individuals—signalers and recipients—exist in all animal communication systems (Wilson 1975, Smith 1977). Signals make information available and recipients use this information when “choosing” a response (e.g., Leger and Owings 1978; Seyfarth et al. 1980a, b). Contextual information, which exists outside signals, is also usually available to recipients and may be appraised by them when selecting a response (Smith 1965, 1977). Consequently, to fully understand the responses of recipients we must identify contextual information in addition to signal-conveyed information.

Vertebrate “alarm” signals (signals emitted in the presence of potential predators) may be multi-functional and appear to vary interspecifically in information content. Some, such as the “hawk alarm” calls of small passerines, may only inform others that a raptor has been detected, but not inform recipients of the hawk’s or the caller’s locations (Charnov and Krebs 1975). In contrast, the alarm calls of other species, including vervet monkeys (*Cercopithecus aethiops*) and California ground squirrels (*Spermophilus beecheyi*), provide extensive information about the type of predator, the location of the caller and even the callers’ age and sex (Seyfarth et al. 1980a, b; Leger et al. 1980; Owings and Leger 1980). Regardless of the type and amount of information contained in alarm signals, it would seem beneficial for recipients to appraise as much contextual information as possible, because of the serious danger posed by predators.

An important form of contextual information for alarm call recipients is the individual’s vulnerability at the time the signal is detected. In fact, recipients of alarm calls do behave differently when vulnerable than when relatively safe (e.g., beaver [*Castor canadensis*] [Hodgdon and Larson 1973], vervet monkeys [Seyfarth et al. 1980a, b], California ground squirrels [Leger et al. 1979], hoary marmots [*Marmota caligata*] [Noyes and Holmes 1979]).

Shorebirds feeding on mudflats adjacent to marshy areas are exposed to attacks by raptors which may use marsh vegetation for concealment during their approach (Rudebeck 1950, 1951; Hunt et al. 1975; Page and Whitacre 1975; Dekker 1980). When they detect predators, shorebirds utter loud calls that usually elicit immediate flock formation and synchronous, erratic flight (Owens and Goss-Custard 1976). “False alarms,” i.e., calls occurring in the apparent absence of predators, are also fairly com-

mon in shorebirds (Leger, pers. obs.). If most attacks by raptors come from the direction of the marsh vegetation, and if the vision of shorebirds is partly occluded by the vegetation, we would expect that individuals closest to the vegetation would be most vulnerable to attack. Thus, individuals hearing alarms while near the marsh should take immediate anti-predator action. Shorebirds farther from the marsh might be able to look around for the predator, and, not finding one, resume foraging. This study was conducted to determine whether shorebirds vary their responses to alarm calls as a function of their distance from the predator-concealing marsh.

METHOD

Subjects and study site.—Response to alarm call playbacks was studied in two species of wintering shorebirds, the Western Sandpiper (*Calidris mauri*) and the Dunlin (*C. alpina*). As the tide recedes, these and other shorebird species assemble to feed on mudflats adjacent to the marsh (Recher 1966). They risk predation by Northern Harriers (*Circus cyaneus*) and Kestrels (*Falco sparverius*), both of which often hunt shorebirds by flying fast and low over the marsh, then suddenly bursting out over the mud to catch their prey by surprise.

This experiment took place in February 1980 along San Francisco Bay at the Baylands Nature Area, in Palto Alto, San Mateo Co., California. The Baylands has a wooden walkway, slightly elevated over the marsh vegetation. At some points the walkway projects out over the mudflat, permitting views of the marsh/mud interface. The specific study site was a section of mudflat with a nearly straight line of marsh vegetation abutting it. Shorebirds at this site seem unresponsive to stationary humans.

Equipment and procedure.—Two months before the experiment, Leger recorded ca. 1.5 sec of alarm calls given by American Avocets (*Recurvirostra americana*) in response to a harrier flying nearby. The recording was made on a Uher 4400 recorder with Uher microphone at 19 cm/sec tape speed. Field observations indicated that such calls usually evoked generalized escape reactions in all shorebirds.

In the morning, before the receding tide had exposed any mud, playback equipment was set up on a section of boardwalk that was elevated about 2.5 m above the mud surface and about 20 m from the marsh vegetation. The playback speaker was oriented from the mudflat toward the marsh. As the water receded, shorebirds began assembling on elevated areas of marsh. As soon as some mud was exposed birds began foraging there. When a 2–3-m strip of mud adjacent to the vegetation was exposed, we began playbacks of either avocet calls ($N = 10$) or a comparable segment of blank audiotape (designated as “no-sound”) as a control for the movements associated with equipment operation ($N = 7$). Playbacks used the Uher 4400 recorder and an Electrosonics “Voice-Projector” amplifier with its integral speaker. Playback volume was adjusted in advance so that it approximated (by ear) that of naturally occurring avocet calls. Immediately before each playback, the area was photographed with a tripod-mounted 35-mm camera (Olympus OM1) equipped with a 100-mm lens and slide film. Immediately after taking the photograph and advancing the film, a playback occurred. Within 1 sec following the end of a playback, a second photograph was taken of the same area. Alarm and no-sound playbacks were alternated with at least 5 min between playbacks. Also, at least 5 min elapsed following naturally occurring alarms of any species, and trials were aborted if an alarm call occurred between the first photograph and the playback.

Because many shorebirds followed the receding tide, only a few playbacks could be done

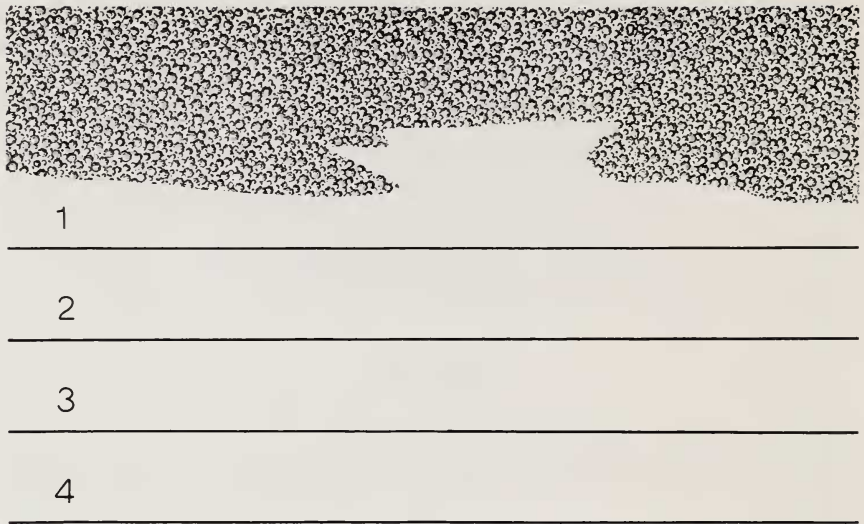


FIG. 1. Outline map of the study site as viewed through the camera. The white area is mudflat and the darker area is marsh vegetation. The parallel lines drawn through the mudflat are ca. 0.5 m apart.

each day before the number of birds in the field of view became too small. Thus, the experiment was conducted on 4 different days during a 3-week period.

Data analysis.—We projected the slides onto outline maps of the marsh and marked the locations of all birds, as well as their postures (head-up or head-down [probing]). We could not obtain exactly the same camera placement each day, so a separate map was drawn for each day's view.

The outline maps (Fig. 1) included straight lines drawn approximately parallel to the edge of the marsh and ca. 0.5 m apart. The distance between adjacent lines was estimated by scaling the standing height of dowitchers (*Limnodromus*) and Dunlins from the slides according to heights measured on mounted museum specimens. From the Dunlin scale the lines were judged to be ca. 53 cm apart; from the dowitcher scale they were ca. 49 cm apart. We used these "strips" to reference birds' locations progressively farther from the marsh. Dependent variables included (1) the number of birds in each strip, (2) the total number of birds, and (3) the percentage of birds in head-up postures. Unless indicated otherwise, statistical tests are 2-tailed *t*-tests for correlated means.

Because it was extremely difficult to consistently distinguish *C. mauri* from *C. alpina* on the slides and because some Least Sandpipers (*C. minutilla*) were probably photographed and counted, our data are for *Calidris* species combined. Larger shorebird species, primarily dowitchers and plovers (*Charadrius vociferus*, *C. semipalmatus*), were also photographed. Unfortunately, the numbers of these larger species varied substantially from day-to-day and their density in the camera's field of view dropped precipitously during a field session (due to the pronounced tendency of dowitchers to forage in the receding water). Therefore, we have too few data on a species other than *Calidris* for meaningful analysis.

TABLE 1
 MEAN NUMBER OF *CALIDRIS* SANDPIPERS ON EACH STRIP OF MUDFLAT BEFORE AND AFTER
 PLAYBACKS OF AVOCET ALARM CALLS OR NO-SOUND (CONTROL) PLAYBACKS

Strip	Alarm call		No sound	
	Before	After	Before	After
1	5.4	2.9*	5.3	6.1
2	5.3	5.0	6.3	5.1
3	2.0	2.1	2.4	2.4
4	1.7	1.0	0.6	0.9

* $P < 0.02$.

RESULTS

Before alarm playbacks ($N = 10$), an average of 14.4 *Calidris* was counted in strips 1–4 combined, and before no-sound playbacks ($N = 7$) a similar mean of 14.6 birds was present in each strip. Birds were not equally distributed among the four strips: strips 1 and 2 averaged 5.4 and 5.7 *Calidris*, respectively, whereas strips 3 and 4 (farther from the marsh) averaged 2.2 and 1.2, respectively. These means differed significantly ($F = 8.64$; $df = 3, 45$; $P < 0.01$ split-plot factorial analysis of variance [Kirk 1968]). However, there was no significant interaction between distance from marsh and playback condition ($F = 0.33$; $df = 3, 45$; NS).

Following alarm playbacks there was an average net loss of 3.4 birds from the total area (from 14.4–11.0), but the mean totals before vs after playback did not differ ($t = 1.08$, $df = 9$, $P < 0.20$). However, strip 1 had only 53.7% as many *Calidris* following alarm calls as before ($t = 2.87$, $df = 9$, $P < 0.02$). Net losses in the other three strips were not significantly different (Table 1). In contrast there was no significant net loss of birds following no-sound playbacks, and none of the before vs after playback comparisons were statistically significant (Table 1). The latter indicates that experimenter movements while operating the camera and playback equipment did not measurably alter the birds' behavior.

Significantly more birds were head-up after alarm call playbacks (68.0%) than before (32.4%) ($t = 2.64$, $df = 7$, $P < 0.05$; two trials were dropped from this analysis because all birds left the field of view following playbacks). In contrast, 29.4% of all birds were head-up after no-sound playbacks, but 45.9% were head-up before. This difference was non-significant, however ($t = 1.36$, $df = 6$, $P < 0.20$). Head-up posturing also varied with distance from the marsh following alarm playbacks. In strips 1 and 2, 69% and 62% of the birds were head-up, respectively, as compared with 38% and 40% in strips 3 and 4.

DISCUSSION

These data suggest that *Calidris* sandpipers monitor their distance from the marsh edge and use this information when responding to alarm calls. It is intriguing that individuals farther from the source of the alarm, but closer to the marsh, reacted more vigorously than did birds in the reverse situation. This finding supports the notion that sandpipers view the marsh as a source of potential danger. Moreover, sandpipers behave as though alarm calls are indicative of danger from the direction of the marsh. At no time did birds fly toward the marsh in response to playbacks or naturally occurring calls. This differs dramatically from the behavior of Yellow-eyed Juncos (*Junco phaeonotus*) foraging at varying distances from a small tree. They use the tree as a refuge, flying to it when alarmed (Caraco et al. 1980). Presumably they would also be more likely to take flight the farther they are from vegetation.

Our data also suggest that there may be some critical distance from the edge of the marsh at which birds can see far enough back over the vegetation to reliably detect an approaching raptor. This distance would vary with the height of the vegetation, the birds' head-up height and the raptor's altitude and approach velocity. We can only speculate on the critical distance here because our measures of location were rather coarse. However, because birds in strip 1 were highly likely to fly or to look up, whereas birds in the second strip tended only to look up, the critical distance for *Calidris* at this site may be ca. 1 m from the marsh. Birds closer than that tend to fly but those farther away tend only to look up, and if a predator is seen, would then undoubtedly fly away. Indeed, naturally occurring appearances of harriers during the study led to all birds in the area taking flight.

Finally, it should be noted that the behavior described above is not restricted to avocet alarm calls, nor to alarm calls at all. Throughout the course of the study many "fly-ups" were observed in response to calls by Willets (*Catoptrophorus semipalmatus*), Marbled Godwits (*Limosa fedoa*), and Killdeer (*Charadrius vociferus*), as well as *Limnodromus* and *Calidris* species. In addition, before conducting this study, Leger observed that *Calidris* sandpipers nearest the marsh were far more likely to fly in response to a single handclap than ones farther from the marsh (but closer to the sound source). Clearly, the marsh seems to be a potent determinant of shorebird behavior.

SUMMARY

Following playbacks of an American Avocet alarm-call recording, *Calidris* sandpipers foraging on a mudflat either flew away from the nearby marsh vegetation, looked up without flying, or continued foraging. The probability of flying and of looking up was highest in birds closest to the marsh, even though they were farthest from the playback speaker. The results

suggest that sandpipers assess their distance from the predator-concealing marsh vegetation and modify their behavior accordingly. Thus, contextual information and information in the alarm call jointly affect sandpiper behavior.

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